THE REACTIONS OF ANTS TO MATERIAL VIBRATIONS.

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While it is well established that some insects react to sound vibrations that reach them through the air, and in this sense may be said to hear, many competent authorities, such as Huber (1810), Perris (1850), Forel (1874, 1900), and Lubbock (1894), have admitted their inability to bring to light any evidence that ants are thus stimulated. Even the discovery of the so-called chordotonal organs in ants by Lubbock (1894) and Janet (1894) has not led to positive results, so far as the reactions of these animals to material vibrations are concerned, though two American investigators, Weld (1899) and Metcalf (1900), have claimed that ants are very sensitive to certain tones.

Because of these somewhat conflicting opinions, it seemed to us desirable to reinvestigate this question,[1] and for this purpose we carried out experiments on the following species of ants:

Camponotine ants:
Camponotus pennsylvanicus (Deg.), workers;
Formica sanguinea Latr., queens and workers;
F. fusca L., var. *subsericea* Say, queens and workers;
Lasius umbratus (Nyl.), queens and workers;
L. latipes (Walsh), workers.

Myrmicine ants:
Stenamma fulvum Roger, var. *piceum* Emery, queens and workers;
Cremastogaster lineolata (Say), queens and workers.

Ponerine ants:
Stigmatomma pallipes (Haldm.), workers.

All these ants had lived more than a month in the artificial nests in which they were tested. They had established their nest-odor, had their young in charge and were well domesticated in their respective abodes.

These ants were tested for two general classes of material vibrations: first, those that reached them through the air surrounding them, and, secondly, those from the solid base upon which the ants rested.

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[1] These investigations were made in the summer of 1903, at the Marine Biological Laboratory, Woods Hole, Mass.

As sources for air vibrations we used a piano, a violin, and a Galton whistle. The keys of the piano gave us a range from 27 to 4176 vibrations per second. The Galton whistle had a range from about 10,000 to about 60,000 vibrations per second, and was provided with a movable threaded core whereby any intermediate vibration could be obtained. The range from the highest note of the piano, 4,176, to the lowest one of the whistle, about 10,000, was bridged over by vibrations obtained from the violin. Thus a series of vibrations from 27 to 60,000 per second were available for experimental purposes.

In testing the ants with these vibrations the artificial nests were so arranged that their air was in free communication with the outer air in which the vibrations were produced, but this was carried out in such a way that draughts, to which ants are very sensitive, could not enter the nests. The nests were placed upon thick paper, so as to isolate them from vibrations that might reach them through the table upon which they rested. The observer then closely watched a quiescent ant under a hand magnifier, while a second person at several metres distance produced the vibrations as desired. As a rule, each key of the piano was struck ten times in slow succession. If the ant under observation seemed to respond, it was given a resting period, and then retested at the pitch to which it apparently reacted. The range of the whistle, 10,000 to 60,000 vibrations, was divided into sixty intervals, and these were treated as the keys of the piano, each note being blown ten times while an ant was under observation. Ants were also watched while the pitch of the whistle was gradually changed by slowly screwing the core either in or out. A gradual change of pitch was also produced on the violin.

All the species mentioned as tested by us were subjected to this range, 27 to 60,000 vibrations per second, and in no single instance was any unquestionable reaction observed. Now and then an ant would seem to respond to a given note, but in every case repetitions of the experiment gave a negative result. We, therefore, conclude that aerial vibrations between 27 and 60,000 per second give rise to no observable responses in the ants we worked upon, and as these included representatives of three subfamilies of the Formicidæ, it is highly probable that a like condition will be found among other ants.

Our results, then, agree with those of Huber, Perris, Forel and Lubbock, but are opposed to what is stated by Weld and by Metcalf. In one instance we worked upon the same species as Weld, namely, *Cremastogaster lineolata*, and tested it with a note approximately that used by Weld (4,096 vibrations), but obtained from the piano and from the violin instead of from a metal bar. Nevertheless we got no reaction. Weld does not make clear that his ants were always isolated from all except aerial vibrations, nor that their reactions were constant under repeated stimulation. It seems to us possible that his ants may have reacted at times to vibrations of the solid base upon which they rested and to which, as we shall show presently, they are very sensitive, or their supposed reactions may have been accidental. Certainly our own experimental evidence gives us not the least reason to suspect that ants are stimulated by sound waves in air.

Having reached this conclusion we next endeavored to ascertain whether ants would respond to vibrations of the solid base upon which they stood. When a nest containing *Stenamma fulvum* was held in the air within a centimetre or so of the woodwork of a piano, and the C, giving 261 vibrations per second, was struck, no response followed. When, however, the nest was allowed to rest on the woodwork and the note was again sounded, almost all the ants started forward simultaneously. Thus a vibration that comes to an ant through the air is not necessarily followed by a reaction, though the same vibration when it reaches the ant through a solid may be very stimulating. All the eight species of ants with which we experimented were thus stimulated, though they failed to react to the same vibrations in the air. The range of the different species was by no means uniform. All reacted to the 27 vibrations per second and to higher notes up to a certain pitch characteristic for each species. *Cremastogaster* reacted at 522, but to no higher note. The superior limit for *Formica fusca*, var. *subsericea* was 1,044, and for *Lasius latipes* and *Stigmatomma* 2,088. *Stenamma* always reacted at 2,088, usually at 3,915, but failed at 4,176. *Camponotus* regularly reacted at 3,480, but failed at 4,176. *Formica sanguinea*, which invariably responded at 2,088, occasionally did so at 4,176, a pitch regularly reacted to by *Lasius umbratus*. Thus each species seemed to have a characteristic superior limit for stimulating vibrations received through solids.

Ants are not only sensitive to the tones of a piano transmitted through a solid, but they are also sensitive to vibrations from other sources similarly transmitted. This is well seen in the following experiment on *Stenamma*. When the edges of two Petri dishes were rubbed against each other in the air, the ants did not respond; but when the edge of the dish in which the ants were held was rubbed even lightly by the edge of another dish, they reacted with great precision. These reactions occurred even when the Petri dish containing the ants was floating on water and the edge of the vessel containing the water was rubbed. Some idea of the delicacy of these reactions may be gained from the fact that ants in a Petri dish resting on a pine table-top reacted to the scratch of a pin on the table at a distance of ten feet from the dish. A measure of the stimulus necessary to call forth the most delicate reaction, usually a jerking movement of the antennæ, was obtained in the following way: A small artificial nest was built on the end of a long board clear of knots and, after the ants had become accustomed to their nest, stimuli were introduced by dropping a shot weighing half a gram on the board at different distances from the nest and from different heights. It was found that the ants reacted to a blow given to the board 4.3 metres (14 feet) from the nest when the shot fell from a height of 15 centimetres (6 inches), but that they did not react when it fell through only half that distance.

Ants not only react to material vibrations received through wood, glass, water, etc., but they will also react to such vibrations when resting on a bit of sponge in an artificial nest or on the soil in which they construct their nests. Thus ants within their natural earth nests may be stimulated by the vibrations of the material on which they stand, though they will not respond to similar vibrations in the air about them.

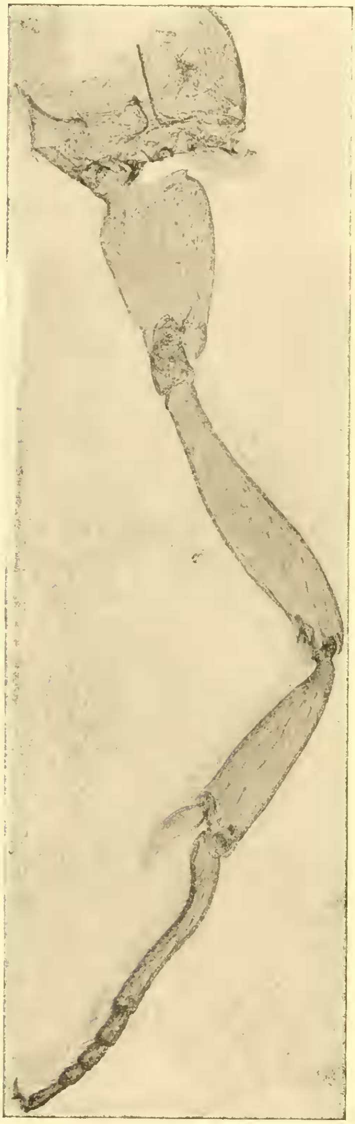
To ascertain what parts of the body of the ant are concerned in its reaction to the vibrations of non-gaseous materials, we performed experiments on a number of individuals of *Stenamma fulvum piceum* that had been deprived of portions of the body.

All the mutilated ants, except those lacking heads or abdomens, had undergone the necessary surgical operations so long as three or four weeks previous to the experiments, and had therefore had time for full recovery from shock-effects.

The irritability of workers deprived of their funicles, or of the whole of the antennæ, was such as to make it necessary to isolate each in order to prevent mutual slaughter, though all were of the same colony. This irritability continued even after they had recovered from shock-effect, had become alert and active, and had been more than a month without funicles, or without both funicles and scapes. Queens similarly mutilated were scarcely more irritable than when in normal condition, and nearly all of the thirty operated upon survived the operation more than two months and laid eggs.

Queens and workers deprived of only one antenna were no more irritable than normal ants, and hardly any deaths resulted from this mutilation, while not more than twenty per cent. of the workers survived the loss of either both funicles or both antennæ.

Queens and workers deprived of a pair of legs, the amputation being made at the coxal joint (see figure), lived in groups as amicably as do whole ants, and there was little loss of life through this operation. The delicate structure of the leg manifestly renders it a probable communicator of vibration from any solid with which it might be in contact.



Prothoracic leg of a young *Stenamma fulvum piceum.* × 48.

There was throughout a direct ratio between the degree of irritability produced and the percentage of deaths consequent upon the surgical operations. The operations were as far as possible carried out aseptically and careful nursing was attempted for all cases.

The mutilated ants were tested in Petri dishes, first by scratching together in the air the edges of two Petri dishes to ascertain whether the ants were stimulated by air vibrations, and next by gently scratching the edge of the dish in which the ants were. As might be expected, no reaction was ever obtained from mutilated ants submitted to air vibrations. The reaction of the ants to the vibrations of the dish containing them and the states of the ants, so far as the operations that they had undergone were concerned, are given in the following summary:

1. Queens from which both funicles had been removed reacted by slight locomotion, usually moving backward or sidewise, rarely forward.

2. Queens from which one antenna had been removed reacted like normal queens by forward, backward or sidewise locomotion.

3. Queens deprived of the whole of both antennæ reacted by moving backward or sidewise.

4. Workers deprived of both funicles moved forward, backward or turned sidewise.

5. Workers deprived of one antenna moved forward or turned sidewise, as did the normal workers.

6. Workers without antennæ moved forward or backward or turned sidewise.

It is thus evident that the antennæ are not essential to the reactions of these ants to vibrations from a solid, for the ants invariably reacted irrespective of the conditions of the antennæ, and the slight differences in the nature of their reactions seem to us insignificant of the function of hearing in parts removed. This opinion, that the antennæ are not essential to these reactions, is in accord with certain observations on normal ants. When a normal ant in a Petri dish was resting with its antennæ high in air, it was observed to react vigorously to a slight scraping on the edge of the dish, without, however, bringing the antennæ in contact with the dish.

7. Decapitated queens and workers reacted by movements of the legs, without, however, showing any determinate form of locomotion.

8. Queens and workers deprived of their abdomens reacted by moving forward or sidewise.

9. Queens deprived of any one pair of legs reacted by moving forward, backward or sidewise.

10. Workers deprived of any one pair of legs reacted by moving forward or turning sidewise.

11. Queens and workers deprived of any two pairs of legs reacted by making ineffectual efforts to walk, their direction of locomotion being very irregular.

It is thus evident that the reactions of the ants to the vibrations of the underlying solid are not dependent upon the antennæ, head, abdomen, any pair or two pairs of legs. It seems to us probable that stimulation is effected by the transfer of the vibration from the underlying solid to the body of the ant, without reference to any special sense-organ. That the various movements of the ants are true reactions, and not merely motions transferred mechanically from the vibrating base to the body of the ant, as to any small particle capable of vibrating, is seen from the fact that the body of a dead ant does not show these movements, and further that in a live ant these movements cease after the stimulus has been repeated a few times, but begin again after the ant has been allowed a resting period of at least ten minutes.

In none of our experiments was there any evidence of a directive influence exerted by the stimulus on the movements of the ant.

The observations and experiments recorded on the preceding pages lead us to conclude that ants are insensitive to air vibrations, such as are audible to us, and that they are very sensitive to the vibration of the solid material upon which they stand, be this wood, glass, sponge or the earth of their nests. These vibrations apparently affect their whole bodies, reaching them through their legs or any other part in contact with the solid base. It is of course conceivable that if an air vibration were strong enough—*i.e.*, if the sound were loud enough—it might stimulate the body of the ant directly, but apparently this is not usually the case; for, as we have already shown, sounds of ordinary intensity, which call forth no response from the ants when they reach these animals through the air, are very effective as stimuli when they reach the animal from a solid base. It therefore seems probable to us that ants in their nests are stimulated, not by the sound waves in the air of the nest, but by the vibrations of the solid parts of the nest itself. Hence the effectiveness of a heavy footstep in the neighborhood of an anthill as contrasted with the ineffectiveness of the human voice in causing an active emergence of the ants. These animals are, as it were, in the condition of a perfectly deaf person who feels through his feet the vibrations caused by a passing wagon, but cannot hear the sound it produces in the air. This sensitiveness of the ants to the vibrations of the base upon which they rest and their insensitiveness to air vibrations is exactly what would be expected from the requirements of their subterranean life as contrasted with that of aerial insects.

Because of the analogy between the ants and a deaf person we do not wish, however, to be understood to deny hearing to ants; neither do we affirm it.

It has long been recognized by physiologists, if not by the scientific public, that touch and hearing in the vertebrates are very closely related. The apparent separateness of these senses in us is due to the fact that the air waves by which our ears are usually stimulated are too slight to affect our organs of touch. If, however, we transfer our experiments to water, we at once meet with a medium in which, as has long been known, vibrations can be both heard and felt. In dealing with a like question among the lower animals it therefore seems to us misleading to attempt to distinguish touch from hearing, and we shall be more within the bounds of accuracy if we discuss the question from the standpoint of mechanical stimulation rather than attempt to set up questionable distinctions based upon human sensations. We therefore prefer to ignore the question of hearing in ants and to restate our conclusion in the form already given, that these animals are insensitive to the ordinary vibrations of air, but are very sensitive to the vibrations of the solid upon which they stand.

It seems to us probable from our experiments that the material vibrations that stimulate ants reach them in this way rather than through the air. Janet (1893; 1896, p. 19) has described an ingenious method whereby the stridulating of ants can be heard by the human ear, and Wheeler (1903, p. 66) has been able to note a faint sound when a large number of stridulating ants are collected in a bottle. Undoubtedly these stridulations are of ecologic importance to an ant community, but it is our belief, based upon our experiments, that what can be heard by the human ear through the air is probably not the vibration that affects the ants, but rather that the stridulation produces a vibration of the solid constituents of the nest, and that this vibration is the effective one in stimulating the inmates.

Summary.

1. The ants experimented upon did not react to aerial sound waves from a piano, violin, and Galton whistle, which collectively gave a range from 27 to 60,000 vibrations per second.

2. They reacted to most vibrations that reached them through the wood, glass, sponge or nest-earth upon which they stood, though different species seem to have different superior limits in respect to the rate of the vibrations.

3. These reactions are not dependent upon the funicles, the antennæ, the head, the abdomen, any pair or two pairs of legs of the ant, but are usually received through the legs, and probably affect the body of the ant as a whole.

4. The stimulation of ants by the vibration of the solid upon which they stand, and not by the vibration of the surrounding air, accords well with their subterranean life as contrasted with the aerial life of most insects.

5. It is misleading to ascribe or deny hearing to ants; they are very sensitive to the vibration of solids, not to those of air; their reactions could be as appropriately described as resulting from touch as from hearing.

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